Crossed with brown normal $yy\overset{\smile}{bl}\overset{\smile}{bl}$ such a yellow would give the following zygotes:

$$\left.\begin{array}{lll} Yy & \widehat{BL}\ \widehat{bl}; & \text{Yellow heterozygous for black and lethal} \\ yy & \widehat{BL}\ \widehat{bl}; & \textit{Black lethal; dies*} \\ Yy & \widehat{bl}\ \widehat{bl}; & \text{Yellow carrying brown normal} \\ yy & \widehat{bl}\ \widehat{bl}; & \text{Brown normal} \end{array}\right\} \textit{commonly.}$$

$$\left.\begin{array}{lll} Yy & \widehat{bL}\ \widehat{bl}; & \text{Yellow carrying brown and lethal} \\ yy & \widehat{bL}\ \widehat{bl}; & \text{Brown lethal; dies*} \\ Yy & \widehat{Bl}\ \widehat{bl}; & \text{Yellow normal heterozygous for black} \\ yy & \widehat{Bl}\ \widehat{bl}; & \text{Black normal} \end{array}\right\} \textit{rarely.}$$

The death of the rare brown lethal individual would not be noticed, for the common death of black lethals would leave a distinct excess of brown normals.

This hypothesis is capable of experimental test and involves a lethal mutation in an entirely new factor which presupposes no generality of the process in all yellows and agoutis; and simply assumes that yellow, when present, hampers the action of the lethal in much the same sort of way that it hampers the activity of the black forming factor in the skin and hair.

The above hypothesis is advanced simply as an additional possibility for test in case something more than chance fluctuation due to random sampling is involved.

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CREPIS—A PROMISING GENUS FOR GENETIC INVESTIGATIONS

To all who are familiar with the recent advances in our knowledge of heredity, which were made possible largely through the investigations of Morgan and others with the fly, *Drosophila melanogaster,* especially to those who have followed the development of the chromosome theory of heredity with its correlative theories of mutation and evolution, the urgent need of extensive corroborative evidence from other animals and plants must be forcibly clear. Although it appears inconceivable that the conclusions reached from the drosophila investigations are not applicable in all their essential features to all animals and plants,

yet it can not be denied that many biologists are not yet committed to the acceptance of these conclusions as of general application. It is obvious that extensive corroborative evidence, derived from other genera of animals and plants, would be of paramount value in firmly establishing these far-reaching conclusions. It, therefore, becomes one, who allies himself with those biologists who believe in the present importance and future promise of this collection of genetic evidence, derived as it is, almost entirely from a single species of insects, to consider most carefully the selection of other material with which to test the various hypotheses that have been proposed in order to interpret the great mass of drosophila data consistently.

It is encouraging to note the energetic efforts of a number of investigators to obtain a corresponding collection of data from other species of *Drosophila*. As yet, however, little more than a beginning has been made, particularly with the genetic investigations on these species, because it is necessary first to find the comparatively rare mutant individuals with which to experiment. No other genus of animals thus far reported upon possesses so many features favorable to genetic study as does *Drosophila*, although it is probable that other of the lower animal groups will in time furnish material just as valuable. In plants, the only species in which genetic analysis has proceeded far enough to establish the identity of a considerable number of hereditary factors or genes, are the garden pea, sweet pea, snapdragon, maize, barley and wheat. In most of these and in some other plants evidence of linkage of characters in inheritance has been obtained, but in none has the number of linked groups been shown to correspond with the number of chromosomes in the germ cell and because of the relatively large number of chromosomes in these species it will probably be some time before any considerable body of corroborative evidence can be accumulated from them.

In addition to a low chromosome number there are several other desiderata which the ideal form for genetic investigations should possess. It must display numerous germinal variations. It must be prolific and easily reared. It should have a short life cycle so as to permit of the maximum number of generations within a given time. Furthermore, in the case of a plant, it should be self-fertile, so as to permit of establishing pure lines; it should be easily hybridized; and it should flourish when grown under glass.

A brief life cycle is extremely important because numerous generations must be raised in order to secure adequate data for the analysis of more complicated genetic problems. In this respect, no sexually propagated flowering plants can compare with the insects. On the other hand, certain highly desirable features possessed by plants are either impossible or very difficult of realization in animals. For example, asexual reproduction can often be resorted to in plants when it is desired to perpetuate a particular individual for comparison with later generations. But the most important point of superiority of plants over insects for genetic study is the greater possibility in plants of securing hybrids between different species. That this advantage should receive considerable weight will be admitted by all who recognize the need of studying hybrids between species having different chromosome numbers. The desirability of such investigations has been mentioned recently by Morgan (1919) as follows:

> The theory that the chromosomes are made up of independent self-perpetuating elements or genes that compose the entire hereditary complex of the race, and the implication contained in the theory that similar species have an immense number of genes in common, makes the numerical relation of the chromosomes in such species of unusual interest. This subject is one that could best be studied by intercrossing similar species with different numbers of chromosomes, but since *this would yield significant results only in groups where the contents of the chromosomes involved were sufficiently known to follow their histories,* and since as yet no such hybridizations have been made, we can only fall back on the suggestive results that cytologists have already obtained along these lines.

I have italicized one clause in the above paragraph in order to emphasize the importance of extensive genetic analysis in those particular species which are to be used in intercrossing experiments. It is not sufficient that the species have low numbers and different numbers; it is also necessary that the inheritance of a sufficient number of characters in each species be studied so as to establish the linked groups of characters or genes corresponding to the chromosomes of each species. Only then can the contents of the chromosomes involved be sufficiently known to follow their histories in the hybrids.

Thus we find several excellent reasons for seeking among plant materials for a group of species which possess as many as pos-

sible of those features most favorable to securing the desired results.

With this explanatory introduction let us consider briefly the present state of our knowledge of *Crepis* with reference especially to its promise of usefulness in genetic studies.[1] This genus belonging to the chicory tribe of the Compositæ contains about 200 species (according to Index Kewensis) which are widely scattered, the genus being represented by indigenous species in every continent and in Australasia. Just how great is the diversity in morphological characters within the genus remains to be seen, but the wide distribution of the group as a whole and of some of the individual species would lead one to expect a large number of diverse characters and many different combinations of the same. The descriptive connotation of many of the specific names also indicates a remarkable diversity among these forms. For example, there are giants and pigmies, there are forms with bristly, woolly, floury, and glandular pubescence as well as glabrous forms, there are four or more flower colors and one species is named "bicolor." This expectation has been borne out by such observations on preserved and living specimens as the writer has been able to make. There are annual, biennial and perennial species which should prove to be very interesting forms for interspecific hybridization studies. Finally, within at least two of the individual species, there certainly exists a remarkable diversity of forms.

But it is not for its wealth of variation alone that this genus is especially interesting to geneticists. The cytological investigations which have been made on a dozen or more species of *Crepis* reveal a most interesting situation as regards chromosome numbers. There is at least one species (possibly two or three) having only 3 for the haploid number of chromosomes, a group of six or seven species with 4 chromosomes, another group of four species with 5, a single species with 8, another with 9, and still another with 20 chromosomes as the reduced number. The absence of a common denominator greater than one for this series of numbers has caused some interesting speculations as to the method of derivation of one species from another (Rosenberg, 1918). Several cytologists have also noted the fact that the chro-

[1] This paper is a preliminary communication offered mainly for the purpose of calling attention to this promising material. A few species have been under investigation at the University of California for about three years and will be discussed more fully in a future publication.

mosomes themselves in these species are unusually favorable objects of study, one of my correspondents going so far as to predict that in time *Crepis* will become as famous and useful for laboratory work as *Ascaris* is to-day. But the important consideration in the present discussion is the fact that we have here several species with the same chromosome number as *Drosophila melanogaster* and at least one species with one less chromosome pair. Obviously, if some of these species with the smallest chromosome numbers are highly variable, existing in a large number of distinct varieties or forms, they should serve as excellent material for genetic study especially if they possess the other advantageous features already mentioned.

For at least two such species I can report very great promise as objects of genetic research. *Crepis capillaris* (*virens*)[2] with three chromosome pairs (Rosenberg, 1909, 1918; Digby, 1914) and *C. tectorum*[3] with four pairs (Juel, 1905; Rosenberg, 1909, 1918) both exhibit polymorphism to a remarkable degree. This is evidenced by the diversity of forms referred to these species in the herbaria of the Royal Botanic Gardens at Kew and of the Museum of Natural History in Paris. In both species it seems to be merely a matter of sufficiently extensive seed collection that is required in order to secure a sufficient number of allelomorphic pairs of characters to make possible the desired genetic analysis. My cultures of *C. virens*, which have been grown from seed secured from various foreign countries as well as in California, have already yielded several pairs of contrasted characters which will soon furnish a nucleus of genetic data on this species.

These two species are also very prolific, considering the plant as a whole, there being several or many heads on a plant and each head bearing 5 to 15 fertile achenes in *virens* and 30 to 40 in *tectorum*. Unfortunately an individual flower produces but a single seed and the flowers are so small as to make the work of hybridization rather tedious when absolute control is exercised through castration of the unopened flower. But, while this method is essential in original crosses, it usually is not necessary to castrate many flowers for any one cross, and when it comes to

[2] The nomenclature of this species is somewhat in doubt. Both Robinson and Fernald (1908) and Britton and Brown (1918) name it *C. capillaris* (L.) Wallr., but certain European botanists seem to have retained the name *C. virens* L. for this species.

[3] *C. tectorum* L.

making back crosses on a large scale, it may be practicable to depollinate the flowers of the intended female parent with a water jet instead of actually castrating the buds.

As regards other desiderata to be considered in selecting material for genetic study these two species are very promising. They are easily reared in greenhouse or field, the seeds germinating quickly in glass germinators, thus permitting easy manipulation and careful checking of viability when desired. The life cycle varies from three to six months except in rare cases of retarded development and little or no rest period is necessary in the seed stage, so that it is possible to grow two or three generations in a year with proper facilities for culture under glass. Partial or complete self-fertility is the rule in both these species, although in some strains of *virens* the individual plant is nearly self-sterile. No evidence of parthenogenesis or apogamy has been found in these species. In general, therefore, it will be possible to secure numerous sexually propagated pure lines, differing from one another in one or more allelomorphic pairs, which will serve as the basic material for working out the "chromosome content" in these species. It is only the problem of securing seed from a large number of different localities and of growing and carefully studying a sufficient number of plants that must be solved in order to furnish the pure lines desired. The sooner this can be accomplished the sooner can the extensive analysis of the chromosome content of these species be gotten under way. Finally the critical question as to whether these two species can be hybridized has been answered in the affirmative by the preliminary experiments of the present year.[4]

Sufficient has been said, I trust, to convince the reader that we have in *Crepis* a wealth of material which may fairly be expected to furnish data of the greatest value in testing the generality of the chromosome theory of heredity, and that this group is unique in the promise it holds of carrying out that test in much shorter time than would be required if we should depend only on the data which is slowly accumulating from other plants now under investigation. It should be clearly realized, however, that to accomplish the results aimed at, even with *Crepis*, will require a considerable period of time, the length of the period being largely conditioned by the number of investigators attacking the

[4] Since the above was written difficulty has been encountered in inducing these hybrid seedlings to develop beyond the cotyledon stage. If this difficulty can not be overcome both species will be crossed with still other species having low chromosome numbers.

problem and the facilities at their disposal or, in other words, upon the amount of funds available for this project.

In order to advance the genetic analysis of *Crepis virens* and *C. tectorum* now under way to a stage favorable to carrying out the interspecific hybridization studies properly, calls for greenhouse equipment, technical assistance, supplies and labor which are not at present available. Some provision for the collection of seed in foreign countries should also be made. There is no prospect at this time that these facilities will become available in the near future. It is recognized that the expansion of this project will require a larger proportion of the time of the two investigators now engaged on it and the workers concerned stand ready to meet this requirement.

My purpose in going thus into detail is two-fold. First, so far as I am aware, no other geneticists are working extensively with this genus, and it should be clearly understood that under existing circumstances there is little prospect of rapid progress with my own investigations. Yet the work has gone far enough to accumulate material of very great promise. It is hoped, therefore, that means will be found to support adequately the investigations of *Crepis virens* and *C. tectorum* now under way. Second, it is highly desirable that other geneticists also contribute to the analysis of the two species named above and especially that they proceed with similar investigations, accompanied of course with cytological studies, on other species of *Crepis*.

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